

Oystercatcher Predation and Limpet Mortality: The Importance of Refuges in Enhancing the Reproductive Output of Prey Populations

by

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Abstract. On the rocky shores of seabird-breeding islands in Saldanha Bay, South Africa, the limpet *Patella granularis* is preyed upon by African black oystercatchers, *Haematopus moquini*. Limpets escape predation as a consequence both of the development of foliose algae on their shells, and of their rapid growth rate which results in their growing too large for oystercatchers to handle efficiently. Both these factors significantly enhance the probability of limpet survival. Although these means of escaping predation probably are coincidental and not evolved adaptations, they may contribute to the persistence of the limpet population through the reproductive output by large and fecund individuals. On adjacent mainland shores, where limpet and algal production rates are slow, oystercatchers are all but absent from the intertidal system.

INTRODUCTION

Birds are important predators in many intertidal communities and their removal of large numbers of prey items (GIBB, 1956; FEARE, 1966; BAIRD *et al.*, 1985) may result in severe depletion of the food resource (FEARE, 1969; O'CONNOR & BROWN, 1977; GOSS-CUSTARD, 1980; GOSS-CUSTARD *et al.*, 1980; FRANK, 1982). In addition, the preference of avian predators for certain prey size classes and morphotypes may modify prey population demography and reproductive output (GIESEL, 1970; HARTWICK, 1981; HOCKEY & BRANCH, 1983, 1984; BRANCH, 1985; LINDBERG *et al.*, 1987; MARSH, 1987).

In some instances intense avian predation on populations of rocky intertidal invertebrates has contributed to the evolution of adaptations that enable prey to escape detection and capture. For example, in some areas, the intertidal limpet *Lottia digitalis* (Rathke, 1833) (= *Collisella digitalis*) actively seeks vertical and overhanging rock faces,

inaccessible to avian predators, on which to attach in the presence of American black oystercatchers, *Haematopus bachmani* (Audubon, 1838) (HAVEN, 1971; HAHN, 1985). The activity patterns of *Lottia limatula* (Carpenter, 1864) (= *Collisella limatula*) and *Collisella scabra* (Gould, 1846), and the homing behavior of many species of gastropods, have been shown to enhance survival in the face of predation (WELLS, 1980; GARRITY & LEVINGS, 1983). In addition, many intertidal prey organisms are cryptic and avoid detection by virtue of homochromy with the substratum (MERCURIO *et al.*, 1985), or mimicry of a common but inedible species (HOCKEY *et al.*, 1987).

Prey organisms may also escape predation by having refuges in space and size. Although not necessarily evolved adaptations, these means of escape may have a significant impact on prey population dynamics (TAYLOR, 1984). On the rocky shores of seabird-breeding islands in Saldanha Bay, South Africa, African black oystercatchers, *Haemat-*

opus moquini (Bonaparte, 1856), occur at some of the highest densities recorded (HOCKEY, 1983). At the three major islands in the Bay (Malgas, Jutten, and Marcus islands) the densities range from 25 to 78 birds per km of coast. Intertidal limpets are important prey of these resident, territorial predators (HOCKEY & UNDERHILL, 1984), and their estimated annual removal of *Patella granularis* (L., 1758) from the shores of Jutten Island is 1.1 million individuals per km of coast (HOCKEY & BRANCH, 1984).

However, because oystercatchers prefer limpets of between 20 and 40 mm in length (HOCKEY & UNDERHILL, 1984), larger limpets have a refuge from predation. In addition, some limpets inevitably settle in, or move to, positions that render them inaccessible to oystercatchers (*e.g.*, on vertical rock faces or the sides of crevices), thus attaining a refuge in space. The shores of seabird-breeding islands in Saldanha Bay support numerous foliose algae, which have a rapid rate of production in response to nutrient enrichment of intertidal waters by the dissolved guano of seabirds (BOSMAN & HOCKEY, 1986). Foliose algae also develop on the shells of *Patella granularis* which may, as a consequence, be totally hidden from view. This crypticity, although transient and not genotypic in origin, may be expected to enhance limpet survival in the presence of visually hunting predators.

In this study we assess the roles played by crypticity and refuges in size and space in enhancing the survival of limpets at sites with different levels of predatory pressure. None of these means of escaping predation necessarily represents an evolved adaptation and any influence on limpet survival rates may be merely coincidental. However, the escape from predation of certain elements of the prey population has potential long-term implications for prey population dynamics.

METHODS AND MATERIALS

Study Sites

Seven intertidal study sites in the Saldanha Bay area (Figure 1) were visited monthly between December 1982 and April 1984. Three sites were on the shores of rocky, seabird-breeding islands (Malgas, Jutten, and Marcus islands). These sites are washed by nutrient-rich water, a consequence of the run-off of quantities of dissolved seabird guano (BOSMAN *et al.*, 1986). The rate of intertidal algal production on Jutten and Marcus islands is enhanced in response to this nutrient enrichment (BOSMAN & HOCKEY, 1986).

Two study sites (Mauritz Bay and Cape Columbine) were on the mainland shores outside the Bay (Figure 1), where no permanent aggregations of seabirds occur. Intertidal waters at these sites have relatively low nutrient concentrations, and the production rates of intertidal algae are slow in comparison with island sites (BOSMAN *et al.*, 1986; BOSMAN & HOCKEY, 1986). Two additional study sites were on mainland shores within the Bay (North Bay and Bomgat) and, although neither had regular aggre-

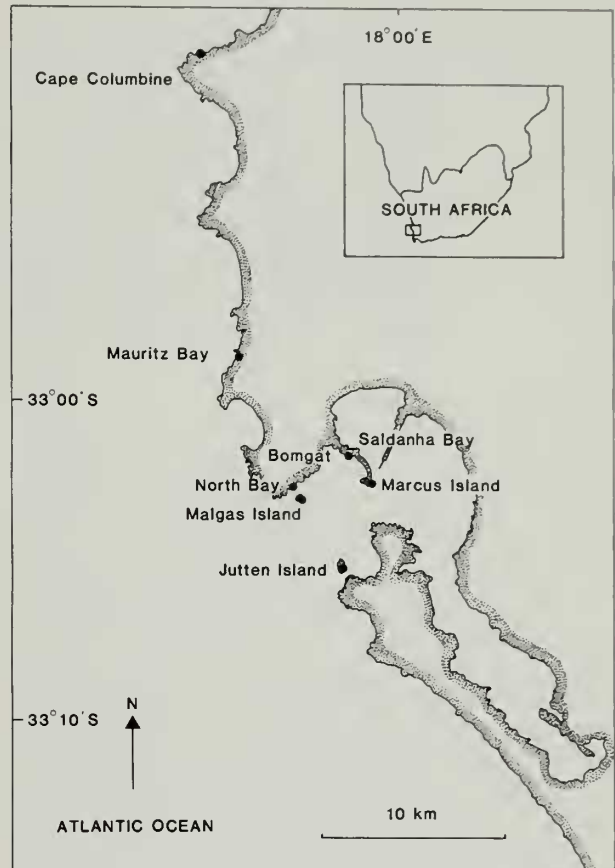


Figure 1

Map of the southwestern coast of South Africa, showing the Saldanha Bay area and the seven intertidal study sites.

gations of seabirds, both were considered to be within the possible zone of influence of nutrient enrichment from the seabird-breeding islands. The North Bay site has nutrient-rich intertidal waters as a result of current movement that transports guano run-off from Malgas Island to North Bay (BOSMAN & HOCKEY, 1986).

At all sites the granitic shore was gently sloping and exposed to strong wave action. Intertidal macroalgae comprised two dominant species—*Enteromorpha* sp. and *Porphyra capensis* (Kütz., 1849)—and the dominant intertidal herbivore (in terms of numbers and biomass) was the limpet *Patella granularis* (see STEPHENSON & STEPHENSON, 1972, for detailed description of intertidal communities). At unenriched mainland sites, where intertidal algal growth is slow, grazing by limpets prevents the development of foliose algae. In contrast, the intertidal algae at nutrient-rich sites form extensive, permanent mats (BOSMAN & HOCKEY, 1986). This is attributable both to the more rapid rate of algal production on island shores, and to the higher densities on these shores of oystercatchers, which remove *Patella granularis* (HOCKEY, 1981) and thereby may reduce the extent of herbivory.

All the sites except Mauritz Bay and Cape Columbine fall within areas of restricted access to the general public. Entry is by permit only and is strictly controlled. Mauritz Bay and Cape Columbine are accessible to the public, but are in areas of low human density. Local people on the west coast of South Africa do not exploit intertidal shellfish on a subsistence or a commercial basis (HOCKEY, in press; HOCKEY & BUXTON, in press) and disturbance to the limpet populations at Mauritz Bay and Cape Columbine is likely to be minimal. Fishermen and crayfish-divers were observed at these sites regularly but in low numbers.

Survival Rates

Each study site was divided into a low-, mid-, and high-shore region of equal area. In each region 50 *Patella granularis* were individually marked using punched plastic labels and rapidly setting epoxy glue. In subsequent months surviving individuals were located. If a limpet was absent in one month, but was located in a subsequent month, it was considered to have been present all the time. If a missing limpet was not located again it was considered dead. Limpets suffered mortality from predation and other factors, and when the number of marked individuals in any shore region fell below 10, supplementary limpets were labelled. The number of marked limpets present each month was used to estimate the finite rate of mortality per month and per year, using equations given by CAUGHLEY (1978). To test the durability of labels, 50 empty *P. granularis* shells were glued to the rock adjacent to the Marcus Island study site and were labelled *in situ*. The loss of labels was monitored during the subsequent seven months.

Influence of Limpet Size and Accessibility on Survival

Each month the shell lengths of surviving limpets were measured, and subsequently the survival rates of individuals smaller than 50 mm in length were considered separately from those of larger individuals. In addition, from April 1983 onwards, the position of each surviving limpet was recorded, and the mortality rates of those accessible to avian predators were considered separately from those of inaccessible individuals. Accessibility was determined subjectively using a knowledge of the morphology and feeding techniques of African black oystercatchers (HOCKEY, 1981). Oystercatchers were considered able to reach limpets on vertical or steep rock-faces if the limpets were less than 17 cm below the top (based on the depth to which oystercatchers reach to obtain limpets in rockpools—Hockey, unpublished data), or less than 40 cm from the bottom (based on the mean height and bill length of oystercatchers) of the rock-face. Accessibility was, however, ultimately determined in the field, as the presence of nearby rocky ledges on which birds could stand often made limpets on vertical rock-faces accessible. In cases where the accessibility of a limpet could not be ascertained clearly, the limpet was excluded from the analysis.

The influences of size and accessibility on the probability of a limpet's surviving for one month were determined using a generalized linear model (McCULLAGH & NELDER, 1984) with a binomial error distribution and logit link function. The data were fitted using GENSTAT 4 (ALVEY *et al.*, 1983). The number of individuals present at the start of the month was equated with the number of trials, while the number surviving the month represented the number of successes. The roles of the independent variables in explaining variation in the probability of survival were expressed as a linear sum of the effects of each variable. The form of the model is thus

$$P = \frac{e^a}{1 + e^a}$$

where P is the probability of surviving one month and $a = b_0 + \sum_{i=1}^n b_i x_i$, where b_i are regression coefficients calculated by the model, and x_i are the explanatory variables, in this case study site, shore region, limpet size, and limpet accessibility.

Influence of Limpet Crypticity

Each month, between April 1983 and March 1984, the amount of foliose algal growth on the back of each relocated limpet was assessed in terms of the percentage of shell that was obscured from view. Percentages were grouped into categories 0, 1, and 2, being respectively, 0%, 1–50%, and >50% covered with algae. Seasonal trends in the proportions of limpets in each category at each site were analysed (with low-, mid-, and high-shore limpets considered together).

The influence of algal cover on the survival of small (<50 mm in length), accessible limpets also was determined using a generalized linear model with a binomial error distribution (see above). In this case the explanation of variation in the dependent variable (probability of surviving one month) is attempted using variations in the independent variables study site, shore region, and percentage algal cover.

RESULTS

Limpet Survival Rates

The plastic labels used to mark limpets were very durable: no labels were lost from the sample of 50 empty shells glued to the rocky shore, although entire shells were occasionally washed away. In some instances live limpets still bore their individual labels two years after being marked. Limpet survival rates measured at the study sites range from 94% month⁻¹ (47% year⁻¹) in the mid-shore regions at Mauritz Bay and Malgas Island, to 77% month⁻¹ (4% year⁻¹) in the low-shore region at the Marcus Island site (Figure 2). Limpets at the Jutten and Marcus Island sites have the lowest probability of survival (in all three

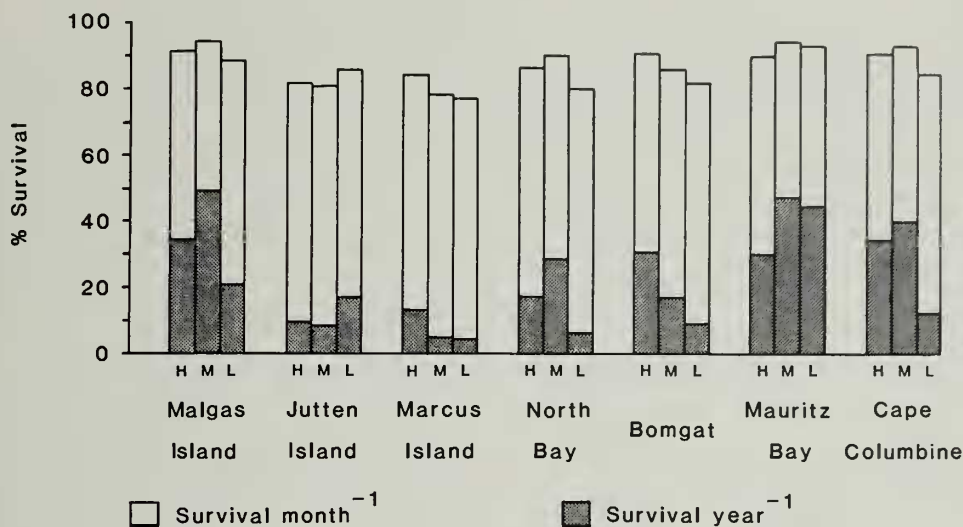


Figure 2

Survival rates of *Patella granularis* in the high- (H), mid- (M), and low-shore (L) regions at study sites in the Saldanha Bay area. Rates are calculated using mark-recapture techniques applied monthly over 12 months.

shore regions), while survival generally is highest at the mainland sites outside the Bay (Figure 2). Limpet survival rates recorded on the shores of Malgas Island are unexpectedly high, given the proximity of dense populations of oystercatchers.

Influence of Limpet Size and Accessibility

The generalized linear model best explaining variations in limpet survival rates ($X^2_{28} = 38.62$, $P > 0.10$) incorporated the independent variables study site, shore region, limpet size, and accessibility, as well as factors that accounted for interactions between site and region, and between site and limpet size (Table 1). The most significant correlate of limpet survival rate is limpet size (d.f. = 54, $t = 5.52$, $P < 0.005$ —Table 1), indicating that limpets measuring 50 mm or more in length have an enhanced probability of survival. The survival of inaccessible and accessible limpets is not significantly different. The shore region in which a limpet occurs also influences its probability of survival. Limpets in the mid-shore region have significantly enhanced predicted survival rates (d.f. = 56, $t = 2.99$, $P < 0.002$) when compared with those in the low-shore region. In contrast, predicted limpet survival in the high-shore region is significantly reduced (d.f. = 56, $t = -1.91$, $P < 0.05$) when compared with survival in both other regions.

Although the relationships described above are applicable to all the study sites considered, the patterns may be modified by the unique influence of each study site. For example (see Table 1), the predicted probabilities of survival of limpets at the three island sites (Malgas Island coefficient is 0.00) are lower than at any other site, irrespective of the shore region involved or the sizes of the limpets concerned. Consequently, the predicted survival of

limpets in different shore regions will be affected by differences between the sites. Similarly, although larger limpets are predicted to have a higher probability of survival, this relationship will be tempered by the unique influence of the site. This accounts for the importance of the interaction factors.

The benefit afforded a larger limpet, in terms of enhanced survival, decreases (coefficient becomes more negative) from island to mainland sites (see "Interactions" in Table 1). This is demonstrated clearly when the influences of all variables are taken into account and the survival rates (as predicted by the model) of limpets at island and mainland sites are compared (Table 2). Large limpets at island sites have consistently higher predicted probabilities of survival than do small limpets, whereas at mainland sites large limpets have reduced probabilities of survival. No limpets measuring more than 50 mm in length were recorded at Cape Columbine.

Influence of Algal Cover

On the shores of islands in Saldanha Bay the proportion of small, accessible limpets that are more than 50% covered by foliose algae peaks in the summer months, particularly between November and January (Figure 3). During the winter months most limpets are free of algal cover, although generally a few individuals support foliose algae in all months of the year. In contrast, limpets on mainland shores outside the Bay seldom support any foliose algae on their shells.

The generalized linear model initially used to explain variations in the survival rates of small, accessible limpets included the independent variable percentage algal cover, which was divided into categories 0, 1, and 2, being 0%, 1–50%, and >50% covered respectively. This model pre-

Table 1

Estimated coefficients, standard errors (SE), and significance levels generated when a generalized linear model is fitted to limpet survival rate data obtained from accessible and inaccessible limpets of two size classes: large are >50 mm and small are <50 mm in length.

Independent variable	Coefficient	SE	<i>t</i>	<i>P</i> (two-tailed)
Constant	1.01	0.161	6.84	<0.0005
<i>Site</i>				
Jutten Island	0.627	0.217	2.89	<0.005
Marcus Island	-0.225	0.225	-1.00	
North Bay	0.928	0.264	3.77	<0.0005
Bomgat	0.667	0.227	2.94	<0.002
Mauritz Bay	1.243	0.270	4.60	<0.0005
Cape Columbine	1.449	0.305	4.75	<0.0005
<i>Shore-Region</i>				
Mid-shore	0.771	0.258	2.99	<0.002
High-shore	-0.402	0.211	-1.91	<0.05
<i>Limpet Size and Accessibility</i>				
Large limpets (>50 mm)	1.112	0.201	5.52	<0.0005
Inaccessible limpets	0.137	0.171	0.80	
<i>Interactions</i>				
Jutten mid-shore	-1.116	0.334	-3.34	<0.001
high-shore	-0.788	0.280	-2.81	<0.005
Marcus mid-shore	0.030	0.339	0.09	
high-shore	0.899	0.295	3.04	<0.002
North Bay mid-shore	-0.208	0.435	-0.48	
high-shore	0.109	0.321	0.34	
Bomgat mid-shore	-0.507	0.352	-1.44	
high-shore	1.266	0.344	3.68	<0.0005
Mauritz mid-shore	-0.563	0.397	-1.42	
high-shore	0.578	0.354	1.63	
Cape Columbine mid-shore	-2.188	0.451	-4.85	<0.0005
high-shore	0.011	0.398	0.03	
Jutten large limpets	-1.017	0.277	-3.68	<0.0005
Marcus large limpets	-1.027	0.297	-3.46	<0.0001
North Bay large limpets	-1.928	0.414	-4.65	<0.0005
Bomgat large limpets	-1.942	0.351	-5.51	<0.0005
Mauritz large limpets	-1.753	0.386	-4.54	<0.0005

dicted no significant difference in the probability of survival of category 0 and 1 limpets (coefficient = -0.002, d.f. = 56, $t = -0.02$) and consequently the data for these two categories were combined. The generalized linear model best fitting the data ($X^2_{36} = 41.04$, $P > 0.20$) incorporated the independent variables study site, shore level, and percentage algal cover (0-50% or >50%) as well as a factor representing the interaction between site and shore region (Table 3).

Limpets that are more than 50% covered by foliose algae have a significantly enhanced monthly survival rate in comparison with limpets supporting less or no foliose algae (d.f. = 56, $t = 1.67$, $P = 0.05$). In addition, survival rate is highest in the mid-shore region (d.f. = 56, $t = 2.47$, $P < 0.01$) and lowest in the high-shore region (d.f. = 56, $t = -1.77$, $P < 0.05$), as was found in the previous model.

Differences in attributes of study sites explained the largest amount of variation in survival rates (Table 3), with the predicted probability of survival being lowest at Malgas (coefficient = 0.00) and Marcus islands, and highest at Mauritz Bay. Limpets at Cape Columbine have an unexpectedly low probability of survival, but when all independent variables are taken into account the interaction between site and shore region compensates for this (Figure 4). Limpet survival rate, as predicted by this model for each shore region at each site, is enhanced in the case of limpets that are more than 50% covered by foliose algae (Figure 4). The predicted benefit to algal-covered limpets, in terms of enhanced survival, is greater at island sites than at mainland sites (Figure 4), with the benefit being least (an increase of 1% in predicted monthly survival rate) in the high- and mid-shore regions at Cape Columbine.

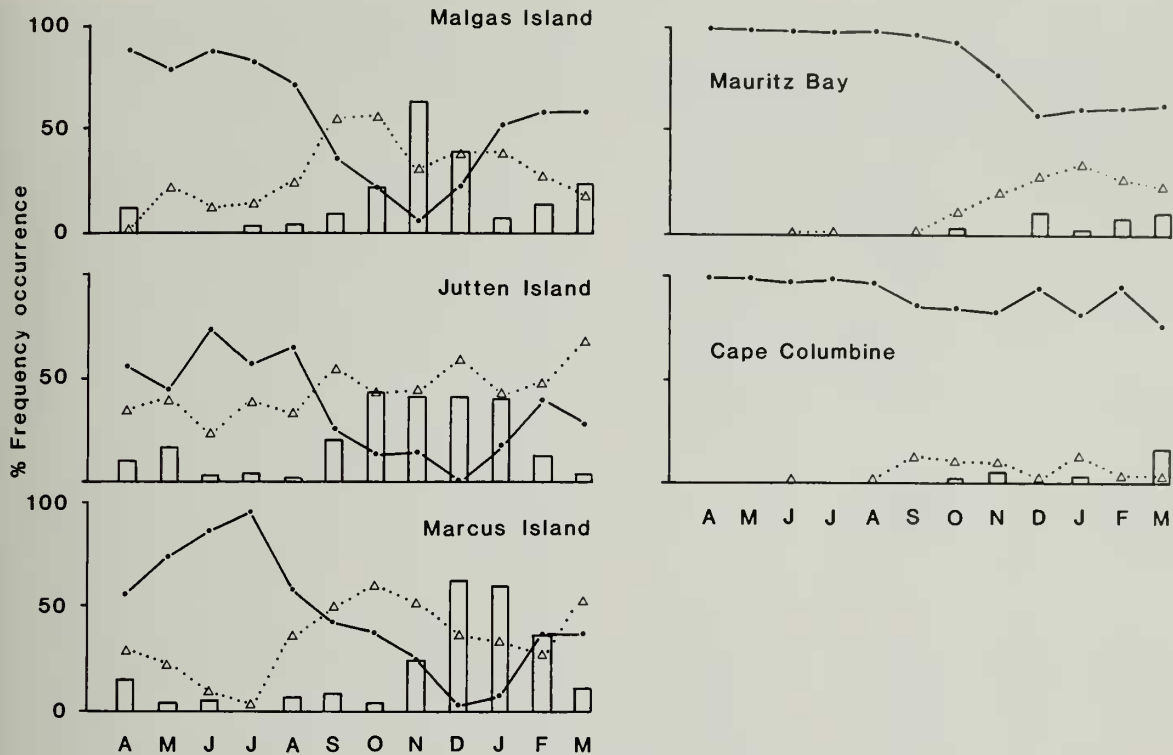


Figure 3

Seasonal changes in the proportions of *Patella granularis*, on island and mainland shores, that support 0% (solid line), 1–50% (dotted line), and >50% (histograms) algal cover on their shells.

DISCUSSION

Limpet Survival Rates

Patella granularis is the most abundant species of limpet in the mid- and high-shore regions of rocky shores on the west coast of southern Africa. It is prominent in the diet of African black oystercatchers, comprising between 24 and 90% of all prey items fed to chicks on the islands off the west coast (HOCKEY & UNDERHILL, 1984). In addition, oystercatchers affect the density and population size structure of limpets accessible to predation on the shores of these islands (HOCKEY & BRANCH, 1984), indicating the major impact of predation by these birds. Other potential predators of *P. granularis* include kelp gulls, *Larus dominicanus* (Licht., 1823), and the giant clingfish, *Chorisochismus dentex* (Pallas, 1769), but limpets are eaten only occasionally by these species (STOBBS, 1980; ARMSTRONG, 1984). The density of African black oystercatchers on islands in Saldanha Bay ranges from 25 (winter count on Malgas Island) to 78 birds per km coast (summer count on Jutten Island—HOCKEY, 1983). In comparison, the mainland coast in the area of the North Bay and Bomgat sites supports between 2 and 16 birds per km coast, and mean density of oystercatchers recorded on mainland shores outside the Bay is 3.6 birds per km coast (HOCKEY, 1983).

Limpet mortality rates measured in the Saldanha Bay area (Figure 2) are highest on the shores of Jutten and Marcus islands, although these rates are not as high as the mortality rate of *Patella vulgata* (L., 1758) (90% month⁻¹) in the presence of European oystercatchers, *Haematopus ostralegus* (L., 1758), reported by LEWIS & BOWMAN (1975). In their study however, oystercatchers were present in large flocks on rocky shores in Yorkshire on a seasonal and transient basis, whereas African black oystercatchers are resident on the shores of islands in Saldanha Bay. Recorded limpet mortality rates were lowest on the mainland shores at Mauritz Bay and Cape Columbine, and intermediate at the North Bay and Bomgat sites (Figure 2). Variations in the survival rates of *P. granularis* at different study sites may be attributed largely to variations in the density of oystercatchers, and consequently, in predatory pressure.

Within each study site, predicted limpet survival is lowest in the high-shore region, possibly reflecting the more stressful physical conditions prevalent in that region (JERNAKOFF, 1983). Limpets in the low-shore region do not have to contend with high temperatures or desiccation as frequently, since they are submerged for a large proportion of the tidal cycle. However, oystercatchers show a peak in foraging activity at the time of low tide (HOCKEY,

Table 2

Monthly limpet survival rates predicted by the generalized linear model fitted to survival rate data from accessible and inaccessible limpets in two size categories (small are <50 mm, large are >50 mm) in three regions of the shore (H = high-shore, M = mid-shore, L = low-shore).

Site	Shore region	Accessible		Inaccessible	
		Small	Large	Small	Large
Malgas Island	H	0.67	0.86	0.70	0.88
	M	0.87	0.95	0.88	0.96
	L	0.75	0.90	0.78	0.91
Jutten Island	H	0.63	0.65	0.66	0.68
	M	0.80	0.81	0.82	0.83
	L	0.85	0.86	0.87	0.88
Marcus Island	H	0.80	0.81	0.82	0.83
	M	0.84	0.85	0.86	0.87
	L	0.71	0.72	0.73	0.75
North Bay	H	0.85	0.72	0.87	0.74
	M	0.93	0.86	0.94	0.87
	L	0.88	0.77	0.90	0.79
Bomgat	H	0.93	0.86	0.94	0.87
	M	0.88	0.77	0.90	0.79
	L	0.85	0.72	0.87	0.75
Mauritz Bay	H	0.93	0.87	0.93	0.88
	M	0.93	0.87	0.94	0.89
	L	0.91	0.85	0.92	0.86
Cape Columbine	H	0.90	*	0.91	*
	M	0.76	*	0.78	*
	L	0.93	*	0.94	*

* No limpets of greater than 50 mm in length were recorded at Cape Columbine.

1984) and tend to forage at the water's edge (HOCKEY, 1981), rendering low-shore limpets more likely to be removed than mid-shore limpets.

Influence of Limpet Size

The most significant correlate of limpet survival rate is limpet size. African black oystercatchers select limpets of between 20 and 40 mm in length, and are unlikely to be successful in removing individuals of more than 60 mm in length (HOCKEY & UNDERHILL, 1984). Consequently, larger limpets have a refuge in size. This is particularly important on the shores of seabird-breeding islands in Saldanha Bay where limpet growth rate is rapid (BOSMAN & HOCKEY, in press) and individuals soon reach a size at which they are free from oystercatcher predation. At these sites larger limpets are predicted to have enhanced survival rates (Table 2). In particular, limpets on the Malgas Island shores are affected by this relationship as the population at this site is dominated by very small and very large individuals (5.8% are greater than 60 mm in length, whereas at Cape Columbine limpets of greater than 50 mm in length do not occur—HOCKEY & BRANCH, 1984; BOSMAN & HOCKEY, in press). Small individuals (<15 mm in length) are not suitable for labelling and consequently, although limpets larger than 50 mm were labelled in proportion to their occurrence in the population at the Jutten and Marcus Island sites (14% and 13% respectively), the larger limpets constitute 33% of the individuals labelled on the shore of Malgas Island. The survival rate recorded on Malgas Island for the limpet population as a whole is thus artificially high.

In contrast, limpets on mainland shores do not benefit

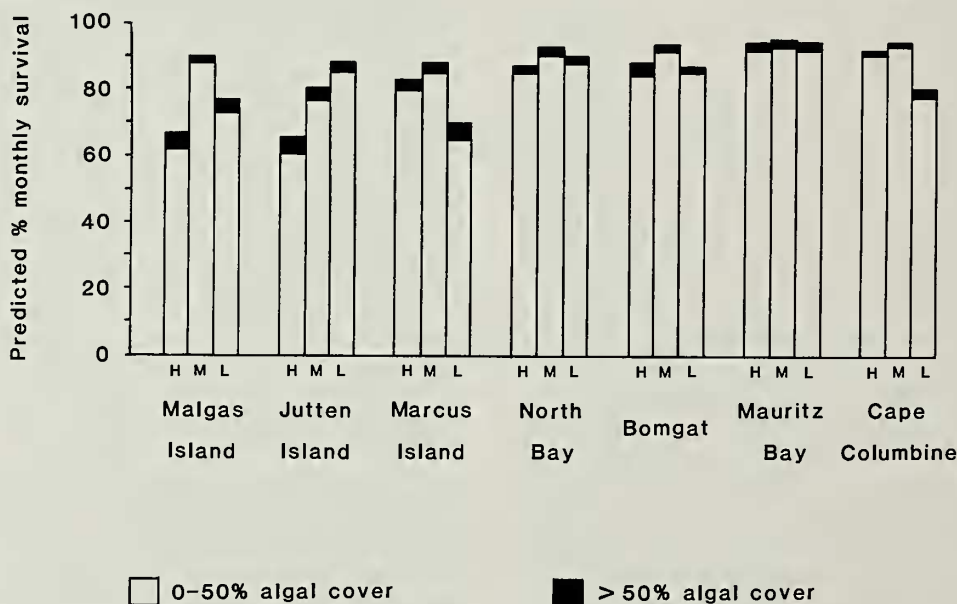


Figure 4

Predicted survival rates of small (<50 mm), accessible *Patella granularis* in the high- (H), mid- (M), and low-shore (L) regions at intertidal study sites. Shaded areas represent the predicted enhancement in survival afforded by a >50% covering of foliose algae.

Table 3

Estimated coefficients, standard errors (SE), and significance levels generated when a generalized linear model is fitted to limpet survival rate data obtained from small (<50 mm), accessible limpets with variable amounts of foliose algae on their shells.

Independent variable	Coefficient	SE	<i>t</i>	<i>P</i> (two-tailed)
Constant	0.990	0.173	5.72	<0.0005
<i>Site</i>				
Jutten Island	0.804	0.232	3.47	<0.0005
Marcus Island	-0.365	0.238	-1.53	
North Bay	0.975	0.251	3.88	<0.0005
Bomgat	0.717	0.236	3.03	<0.002
Mauritz Bay	1.446	0.290	4.99	<0.0005
Cape Columbine	0.245	0.325	0.78	
<i>Shore-Region</i>				
Mid-shore	0.978	0.395	2.47	<0.01
High-shore	-0.495	0.280	-1.77	<0.05
<i>Algal Cover</i>				
>50% cover	0.231	0.138	1.67	=0.05
<i>Interactions</i>				
Jutten mid-shore	-1.564	0.466	-3.35	<0.001
high-shore	-0.858	0.344	-2.49	<0.01
Marcus mid-shore	0.114	0.464	0.25	
high-shore	1.258	0.365	3.45	<0.001
North Bay mid-shore	-0.587	0.517	-1.13	
high-shore	0.273	0.374	0.73	
Bomgat mid-shore	-0.632	0.468	-1.35	
high-shore	0.511	0.548	0.93	
Mauritz Bay mid-shore	-0.793	0.514	-1.54	
high-shore	0.524	0.417	1.26	
Cape Columbine mid-shore	0.318	0.547	0.58	
high-shore	1.510	0.461	3.28	<0.001

by being large, and the predicted probabilities of survival are lower for large individuals than for small ones at the same site (Table 2). Limpets have slower growth rates on mainland shores than on islands (BOSMAN & HOCKEY, in press) and, since maximum adult size attainable by an individual is a function of its growth rate (BRANCH, 1974b; BALAPARAMESWARA RAO, 1976), limpets on unenriched mainland shores never attain sizes comparable with those on islands. Large limpets on an unenriched mainland shore are thus older than similarly-sized individuals on an island shore, and may experience higher mortality due to senescence.

Influence of Accessibility and Crypticity

Limpets inaccessible to oystercatchers automatically achieve a refuge from predation by birds, irrespective of their growth rate and size. *Patella granularis* exhibits homing behavior and will return to a home scar during periods of inactivity and environmental stress, *e.g.*, during the day-time low-tide period (BRANCH, 1971). In this study 89% of limpets that were recorded as being inaccessible in a month, and that survived at least three subsequent months, were recorded as inaccessible on all four visits; yet the

model used predicted no advantage (in terms of limpet survival) to this behavior (Table 1). *Patella granularis* forages at night (BRANCH, 1971) and those individuals recorded as inaccessible during day-time visits to a study site may have become accessible during the night (particularly those on the walls of crevices in the rock). Oystercatchers also forage at night, and HOCKEY & UNDERHILL (1984) showed that on Jutten Island limpets formed a higher proportion of oystercatcher prey items at night than during the day. Given such conditions, few limpets in this study probably were truly inaccessible to oystercatchers.

Oystercatchers forage using visual cues and have been shown to discriminate between the anterior and posterior shell margins when attacking limpets (HOCKEY, 1981; HOCKEY & BRANCH, 1983). Foliose algae that develop on the shell of a limpet and that obscure 50% or more of the individual render it less likely to be recognized as a prey item and significantly enhance its probability of survival. The probabilities of survival of limpets without algae and those with 1–50% cover are not different, indicating that it is the escape from predation afforded by the algal cover, rather than the amelioration of temperature and desiccation stresses, that leads to enhanced survival.

The development of algae on the shells of marine and

intertidal organisms has been documented in several instances (SINCLAIR, 1963; BOUXIN, 1964; BRANCH, 1971) but no advantages have been demonstrated to accrue to affected individuals. In the Saldanha Bay area foliose algae develop on *Patella granularis* shells during the months when rates of algal production are fastest (BOSMAN & HOCKEY, 1986), and the development of algal covering is most profuse and widespread on island shores (Figure 3). The effect of an algal covering on limpet survival rate is apparent (albeit very slight) on mainland shores, but is more pronounced on the shores of islands, where oystercatcher predatory pressure is intense (Figure 4), once again indicating that the primary advantage of an algal covering is the camouflage it provides.

Differential Survival Rates: Their Impact on Prey Population Dynamics

The selective removal of certain prey size classes by avian predators may have a significant impact on the demography and dynamics of the prey population. HOWARD & LOWE (1984) found that selection by royal spoonbills, *Platalea regia* (Gould, 1838), of the largest and slowest-moving caridean shrimps in seagrass beds leads to a disproportionately high mortality of adult females. Females attain larger body sizes than males, and may be hampered, when attempting to escape, by the mass of the large clutch of eggs. There is a resultant skewed sex ratio in the population, and female longevity and life-time reproductive output are reduced. On the rocky shores of islands in Saldanha Bay predation by oystercatchers results in high mortality of medium-sized limpets. However, the rapid growth rates of limpets on island shores, and the inability of oystercatchers to handle large limpets, ensure that a certain proportion of individuals attain a refuge from predation by virtue of their size.

Limpet gamete production increases exponentially with respect to an increase in shell length (BRANCH, 1974a), and HOCKEY & BRANCH (1984) estimate that as much as 86% of the female gametic material released by limpets on the shores of Jutten Island is derived from limpets that have a refuge in size. The reproductive effort of these individuals probably is vital to the system's continued ability to support dense populations of oystercatchers. Oystercatchers are uncommon on mainland shores (particularly outside the Bay) where the rate of limpet growth is slow and even the largest and most fecund limpets would be available to the birds.

The demography and reproductive output of limpet populations on the shores of seabird-breeding islands are modified by the effects of oystercatcher predation. The size structure of prey populations is altered (HOCKEY & BRANCH, 1984), and the average survival rates and lifetime reproductive outputs of individuals are reduced. The reproductive output of the prey population may be maintained by virtue of a refuge in size for large individuals and, to a lesser extent, by the crypticity resulting from the development of foliose algae on the shell of the prey.

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